An experimental test of resistance to cheatgrass invasion: limiting resources at different life stages

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Abstract

Variable densities of an invasive species may represent variation in invasion resistance, due to variation in resource availability. This study determined whether low- and high-density cheatgrass (*Bromus tectorum* L.) patches within a shadscale-bunchgrass community of western Utah, USA, can be explained by variation in resource availability. It also explored the possible role of seed limitation and enemy pressure on invasion patterns. Two parallel field experiments were conducted: (1) increasing resources within low-density cheatgrass patches and, conversely; (2) reducing resources within high-density cheatgrass patches. Treatments were applied at three life stages separately and across all stages. In low-density cheatgrass patches (assumed to represent high resistance), a disturbance that reduced soil compaction had the strongest positive effect, significantly increasing biomass by 250% and density by 104% in comparison to the control. The second strongest effect was reducing neighbors (native grasses), which significantly increased cheatgrass biomass and density. These results indicate that resources are present in low-density cheatgrass patches, but they are unavailable without disturbance and/or are exploited by competitors, and hence represent resistance to invasion. In high-density cheatgrass patches (assumed to represent low resistance), nitrogen availability was important in maintaining cheatgrass densities. Reducing nitrogen (*via* sucrose addition) significantly decreased density (by 37%) but not biomass. Life stages of cheatgrass were differentially affected by these resource manipulations. In addition, herbivore (primarily grasshoppers) and pathogen (head smut) pressures were documented to affect cheatgrass density, but did not explain resistance patterns. Instead, we found that differential resource availability explains the observed variation in cheatgrass density, and variation in natural resistance.

Introduction

Elton (1958) first introduced the concept of 'ecological resistance', the natural processes that negatively influence invasion success. Only recently has resistance to invasion been studied experimentally, primarily in artificial assemblages (e.g., Levine 2000; Prieur-Richard et al. 2000) or highly modified ecosystems (Burke and Grime 1996; Tilman 1997). Although these studies are useful in producing general predictions of invasion, experimental studies of naturally invaded systems are needed to understand the mechanisms controlling resistance for a specific invader.

Stohlgren et al. (1999) suggest that the underlying mechanism for resistance to plant invasion is the availability of limiting resources. Resources may limit an invading species in a variety of ways. Resources may be (1) lacking from the site (Huenneke et al. 1990); (2) present, but exploited by competitors (Hobbs 1989); and/or (3) present, but unavailable without disturbance (Fox and Fox 1986). Available resources may also vary temporally. The ability of a plant to respond to short-duration pulses is dependent on its phenological stage (Bilbrough and Caldwell 1997) and a resource limiting one life stage may not be limiting at another stage (Schupp 1995). Susceptibility to invasion can arise when resource availability shifts towards an increase in unused resources for the invader (Davis et al. 2000) or when the invader's requirement for resources decreases (Tilman 1999).

In the Great Basin, cheatgrass (*Bromus tectorum* L.) has replaced some desert shrub and pinyon-juniper communities as a monoculture (Billings 1990); however, not all areas invaded by cheatgrass become a monoculture. A shadscale (*Atriplex confertifolia* Wats.)-bunchgrass community in western Utah displays local-scale variation in cheatgrass density, making it ideal for an experimental investigation of the relationship between resistance and resource availability. Previously, Beckstead (2001) showed that cheatgrass exists in a mosaic of low- and high-density patches on a scale of < 10 m, intermixed with the native plant community. This mosaic allows a two-pronged approach to evaluate the role of resources in regulating resistance to invasion. If this variation in cheatgrass density reflects a mosaic in soil resources (i.e., low-density cheatgrass patches have relatively low resources, while high-density cheatgrass patches have relatively high resources), then increasing resources in low-density patches will increase the biomass and density of cheatgrass; conversely, reducing resources in high-density patches will decrease the biomass and density of cheatgrass. However, specific resources and the extent to which they regulate cheatgrass biomass and density may or may not be the same in both patch types. If manipulating resources as described above does not induce a response by cheatgrass, then either the incorrect resources were manipulated or other

factors are responsible for the pattern. This study explores whether variable densities of an invasive species may represent variation in invasion resistance, due to variation in resource availability. In addition, seed limitation and enemy pressure may affect invasion resistance; this paper also investigates the role of these other factors on invasion resistance.

Low-density cheatgrass patches could arise from seed, not resource, limitation. Levine (2000) found within a California riparian system at a community-wide scale that propagule supply from outside the system was more important than local diversity in controlling resistance to invasion. At a patch-wide scale in a system where the invader has established, seed limitation may be more likely linked with resource limitation (i.e., plants with limited resources produce fewer seeds). Seed limitation, independent of resources, could occur through (1) seed losses from seed predation; (2) seed losses from seeds emigrating from the patch; and/or (3) restriction of seed immigrating into the patch. Previous studies by Beckstead (2001) found no evidence for seed losses from seed predation or seed emigration and no restriction of seed immigration. These findings indicate that seed limitation, independent of resources, is insufficient to account for the low-density cheatgrass patches.

In contrast to resource or seed limitation, low-density cheatgrass patches could be regulated by biotic agents, such as high herbivore and/or pathogen pressures. The feeding patterns of both specialist and generalist herbivores can create vegetation patchiness (Wiens 1976) and the spread of a disease/pathogen is unavoidably spatial (Holmes 1997). Although these alternative forces were not addressed experimentally in this study, their effects on cheatgrass biomass/density were quantified.

At the study site, specific resources that could limit cheatgrass directly or indirectly were identified from prior studies. First, in greenhouse studies of cheatgrass, low nitrogen and/or water (Dakheel et al. 1993, 1994; Link et al. 1995) lowered cheatgrass biomass; phosphorus was not as influential as nitrogen (Dakheel et al. 1993). Second, greenhouse studies (Aguirre and Johnson 1991; Francis and Pyke 1996) and a field study (Melgoza et al. 1990) found that competition

(reducing water and/or nutrient availability) between cheatgrass and some range species lowered cheatgrass biomass. Thirdly, low litter accumulation reduced water availability, thereby lowering cheatgrass biomass (Stewart and Hull 1949), and reduced cheatgrass densities by increasing secondary seed dispersal (Pierson and Mack 1990). Finally, soil compaction lowered water infiltration (Blackburn 1975); Thill et al. (1979) found that increased soil compaction decreased the percentage and rate of cheatgrass seedling emergence. Each factor may limit cheatgrass, a winter annual, at a different phenological life stage (i.e., establishment, over-wintering, and active-growth).

The goals of this study were to determine experimentally whether differential resource availability explains variation in resistance to cheatgrass invasion (i.e., the low- and high-density cheatgrass patches) and at which life stage resources are most limiting. Two parallel field experiments were conducted: (1) increasing resources within low-density cheatgrass patches and, conversely; (2) reducing resources within high-density cheatgrass patches. Treatments were applied to the same cheatgrass individuals repeatedly at each of three life stages (hereafter, across all life stages) to determine which resource manipulation(s) produced the greatest change in biomass and density of cheatgrass. Furthermore, treatments were applied to cheatgrass individuals once at each of the three life stages to determine which life stage(s) was most affected by the resource manipulation(s).

Materials and methods

Study site and study species

This research was conducted in a native shadscale-bunchgrass community located in western Utah, USA, on Bureau of Land Management land (14 km south of English Village, Dugway Army Proving Grounds; 40°7′ N, 112°40′ W; 1550 m elevation). The study site, a cold desert, has a mean monthly temperature of 18.3 °C; it ranges from 32 °C (June–August) to 5 °C (December–February) (Stevens et al. 1983). Mean annual precipitation is 176 mm; the season with the highest total precipitation (56 mm) is March through May.

The community is dominated by the shrub shadscale and two native perennial bunchgrasses, sandberg bluegrass (*Poa secunda* Presl.) and squirreltail (*Elymus elymoides* Raf.). Other common herbaceous species include Indian ricegrass (*Stipa hymenoides* R. & S.), needle-and-thread (*Stipa comata* Trin. & Rupr.), western wheatgrass (*Elymus smithii* Gould), and Munroe globemallow (*Sphaeralcea munroana* Gray). Nomenclature is from Welsh et al. (1987).

The history of cheatgrass invasion at the site is unknown. Although cheatgrass invaded the Great Basin in the late 1800s (Mack 1981), its widespread invasion into salt-desert shrub communities in general did not occur until the early 1980s, perhaps resulting from extreme wetness related to El Niño followed by wildfires in subsequent years (West 1994). The study site was grazed up to the initiation of the study by domestic livestock (cattle and sheep), wild horses, and antelope (J. Beckstead, personal observation) and was enclosed by a fence to exclude vertebrate herbivores. The long-term fire history of the site is unknown, but there is little evidence of recent fire (J. Beckstead, personal observation).

Cheatgrass, a winter annual of European origin, is the most common and widespread exotic species at the site. In western Utah, its seeds usually germinate from October to November (Beckstead et al. 1995) during the autumn rains. Young cheatgrass plants over-winter in a semi-dormant state (Klemmedson and Smith 1964). Active growth resumes in the spring with the onset of warmer temperatures (Thill et al. 1984) and inflorescences emerge during late April to early May (Hulbert 1955). Seeds ripen in June to July and fall to the ground shortly after maturity (Klemmedson and Smith 1964); seeds experience secondary dispersal by wind and water (Kelrick 1991). Seeds are dormant at maturity and require after-ripening (period of warm, dry temperatures) to germinate at temperate, autumn temperatures when soil moisture is adequate (Beckstead et al. 1996). Cheatgrass seeds do not have a long-term seed bank (Mack and Pyke 1983; Beckstead et al. 1995), although seeds caught in litter are carried over from year-to-year (Kelrick 1991).

For the two-pronged approach of studying both low and high invasion resistance, we arbitrarily set subjective limits for the low- ($<15\%$ cover) and high- ($>85\%$ cover) density cheatgrass patches. For the purpose of experimentation, we chose to focus on the extremes of this continuous variable and assume that the intermediate densities would demonstrate a response to treatment within the range of the low- and high-density categories. Low-density cheatgrass patches covered 25% of the study area and high-density cheatgrass patches covered 30% of the study area (50×100 m; data obtained from aerial photographs taken in 1999). In an adjacent area, semi-variograms showed spatial dependence of cheatgrass densities up to 9 m, averaged across 3 years (Beckstead 2001); this may be interpreted as patch size (Dent and Grimm 1999). Native grass species (i.e., primarily, *P. secunda* and occasionally, *E. elymoides*) are common in low-density cheatgrass patches. Low-density cheatgrass patches contained $54 \pm 16\%$ (mean $\pm$ 1 SD) cover of native grass species and all sampled plots contained native grasses (data obtained in June 1999 for 30×30 cm plots in 10 patches; percent cover for native grasses was assessed by a modified Daubenmire cover-class method; Mueller-Dombois and Ellenberg 1974). In contrast, high-density patches infrequently contained native grass species; 40% (6 out of 15) of high-density patches contained some native species, but only 14% (13 out of 90) of 25×50 cm plots within these patches contained native plant species (data obtained in June 1998). Number of reproductive cheatgrass tillers per dm^2 at the study site from 1997 to 1999 was lower in low- (3, 5, 3, respective years) than in high- (17, 21, 7, respective years) density cheatgrass patches (Beckstead 2001). In an adjacent area at the study site, number of seeds per dm^2 was 13 ± 2.1 and 289 ± 28 (mean $\pm$ 1 SD, $n_1 = 45$, $n_2 = 15$) for low- and high-density patches, respectively (Beckstead 2001).

Herbivore/pathogen pressures

Generalist insect herbivores of the community include resident grasshopper species and the periodically migrating Mormon crickets (*Anabrus simplex* Haldeman), which is a shield-backed katydid and not a true cricket (Pfadt 1994). The redshanked grasshopper (*Xanthippus corallipes* Haldeman) and pasture grasshopper (*Melanoplus confusus* Scudder) are the most common resident insect herbivores of cheatgrass at the site (J. Beckstead, personal observation). In midsummer of 1998, adult Mormon crickets migrated into the site, mated, and laid eggs, which hatched in March 1999 at the start of active growth for cheatgrass. Mormon crickets had not been seen around the site for at least the past 15 years (R. Scheese, personal communication). Mormon crickets have historically, as well as recently, caused heavy herbivory to crop and range plants in the Great Basin, although heavy damage is usually infrequent and localized (Wakeland 1959). In order not to lose the entire experiment, which was already in progress, to the feeding of Mormon crickets, we baited the study area (50×100 m) with 3 l of carbaryl (active ingredient in Sevin™) wheatbran four times from March to June 1999. This selective insecticidal bait differentially kills Mormon crickets but not grasshoppers (Quinn et al. 1989; confirmed by counting carcasses following bait application).

Grasshopper herbivory was assessed in 1999 in multiple 30×30 cm plots in 10 low- and 10 high-density cheatgrass patches. A grid with 12 intersecting points, was inserted onto each plot and the nearest cheatgrass individual to each intersecting point was categorized for herbivory as 'yes' (stem chewed to a stump) or 'no' (stem complete with reproductive structures). We analyzed differences in the percentage of grazed individuals (arcsine transformation to meet normality) per plot between low- and high-density cheatgrass patches as a mixed model one-way analysis of variance (ANOVA) with subsampling, including patch as the fixed effect, replication and replication by patch interaction as random effects, and plots as the subsample (PROC MIXED; SAS 1999).

A frequent pathogen of cheatgrass in the Great Basin is head smut (*Ustilago bullata* Berk; Mack and Pyke 1984). This systemic head smut infects seedlings, stunting plant growth and in most cases eliminating seed production (Alexopoulos et al. 1996). To quantify the smut infection at the study site in 1998, we counted all smut-infected

tillers at the time of seed formation from randomly selected 25×50 cm plots in low- ($n = 30$) and high- ($n = 27$) density cheatgrass patches. We analyzed differences in smut infection (arcsine transformation to meet normality) between low- and high-density cheatgrass patches using a t-test adjusted for unequal variances *via* the Satterwaite method (PROC TTEST; SAS 1999).

Field experiment

Within each patch type, the experimental design was a complete randomized nested design with two factors (life stage and resource treatment). Life stage with treatments (1×2 m area within a patch) was nested within a patch and resource treatments (30×30 cm plot was the experimental

unit; distance between plots was > 30 cm) were nested within each life stage area. Control plots were randomly selected at the patch level. Cheatgrass biomass and density for all treatment-stage combinations were obtained only from final harvest measurements; i.e., application of treatments occurred at each life stage, but harvest did not (Figure 1).

In early June 1998, 10 low-density cheatgrass patches were randomly selected and the nearest 10 high-density cheatgrass patches within the 50×100 m study site were chosen; mean distance from the center of a low patch to the center of the nearest high patch was 11.4 ± 4 m (mean $\pm$ 1 SD; $n = 10$). Within each patch, control plots and four life stage areas were randomly selected; each low-density patch had three control
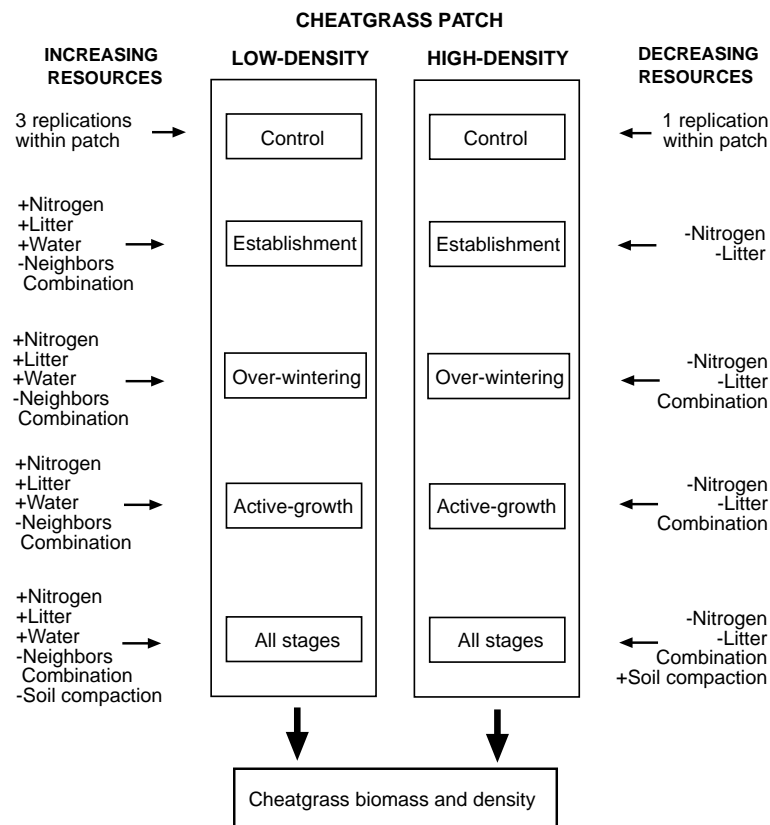

Figure 1. Schematic diagram of experiment. Increasing resources in low-density cheatgrass patches and decreasing resources in high-density cheatgrass patches by adding (+) or reducing (−) factors at three cheatgrass life stages separately (establishment, overwintering, and active-growth) and across all stages (treatments repeated at each of three stages). The control was at the patch level. The combination treatment consisted of all treatments, applied simultaneously to a given plot, except soil compaction (see 'Materials and methods'). All plots were harvested at seed formation to assess the treatment and stage effects on cheatgrass biomass and density.

plots to account for spatial variation in seed source and each high-density patch had one control plot. Treatments were applied to 30×30 cm plots, either increasing resources in low-density cheatgrass patches or decreasing resources in high-density cheatgrass patches (Figure 1). Treatments for a given life stage area were applied at the initiation of its designated life stage of cheatgrass, $viz.$, establishment (late August 1998), over-wintering (November 1998), and active-growth (April 1999). For the fourth life stage area, a given treatment was applied across all stages on a plot (i.e., treatments repeatedly applied at each stage in August, November, and April; hereafter, all stages).

In low-density cheatgrass patches ($n = 10$), treatments increasing the resource availability were (Figure 1): (1) nitrogen addition (5.3 g/m^2 N in NH_4NO_3; level follows McLendon and Redente 1991); (2) litter addition (< 1 cm deep of autoclaved cheatgrass litter from site); (3) water addition (2 l slowly dripped onto plot via holes in a ziploc bag elevated above plot; simulating one 25 mm rain event over 4–5 h; this type of rain event is not uncommon, but on the high end of rain events for the area; July 9, 1998, 23 mm rain event); (4) neighbor reduction (removal of above-ground biomass of native grasses in plots selected with lower native plant cover relative to controls); (5) soil compaction reduction (aeration of top 5 cm; 12 1 cm diameter holes created with a small garden spading fork; this spading resulted in a $10 \times$ reduction in soil resistance measured by a dynamic cone penetrometer; Herrick and Jones 2002); and (6) application of treatments 1–5 combined (hereafter referred to as combination treatment). All treatments were applied to each of the three life stage areas separately and to the all stages area with the exception of the compaction treatment (Figure 1). The compaction reduction treatment was imposed only in August at the initiation of the experiment. The effects of the compaction reduction treatment (likely an increase in infiltration and aeration; Blackburn 1975) were assumed to persist across all stages; thus treatment effects would be conservative if treatment did not persist. The neighbor reduction treatment had two components: (1) clipping of above-ground biomass of neighbors (effects assumed to be temporary for each individual stage); and (2) selection of plots with lower native plant cover relative to controls (effects persisted across all stages). Plots with lower native plant cover were assumed to have lower competition than control plots.

In high-density cheatgrass patches ($n = 10$), treatments decreasing the availability of resources were (Figure 1): (1) nitrogen reduction (addition of 50 g/m^2 of sucrose to increase microbial biomass and, thereby, decrease available nitrogen; Lamb 1980); (2) litter reduction (removal of litter only for the period of a given stage); (3) enhanced compaction (compaction of top 5 cm using 80 strikes with a hand tamper; it resulted in a $2 \times$ increase in soil resistance measured by a dynamic cone penetrometer; Herrick and Jones 2002); and (4) application of treatments 1 and 2 combined (hereafter referred to as combination treatment; missing at the establishment stage). All treatments were applied to each of the three life stage areas separately and to the all stages area with the exception of the compaction treatment (Figure 1). The compaction treatment was imposed only in August at the initiation of the experiment, because compaction at any vegetative stage would have caused serious damage to the plants. For logistic reasons, we did not attempt water reduction or neighbor addition treatments.

Spatial variation in the seed source for each experimental plot could have confounded values of cheatgrass biomass and density. Sources of variation could include a seed bank and the previous year's seed production and seed dispersal. We assumed a greater amount of confounding variation would arise from these sources in low- than in high-density cheatgrass patches. Therefore, we hand-weeded all cheatgrass plants from the experimental low-density cheatgrass patches in June 1998 prior to seed dispersal; care was taken to minimize soil disturbance and most stems broke at ground level, leaving roots in the ground. To simulate natural cheatgrass densities in low-density patches and to ensure that all experimental plots contained cheatgrass seeds, we sprinkled 70 cheatgrass seeds on each treatment plot (30×30 cm) in August 1998 at the beginning of the experiment. This seed density was based on seed production to establishment ratios quantified in 1997 and an estimated 60–70% mortality rate (J. Beckstead, unpublished data).

In June 1999 at the time of seed formation, cheatgrass was counted for density and harvested for above-ground biomass. Harvested plants, including spikelets and seeds, were dried at 60 °C and weighed. Although seed output was not measured directly for each plant, cheatgrass seed number is highly correlated with biomass (Hulbert 1955). Similarly, Beckstead (2001) found at the same study site in both low- and high-density cheatgrass patches that seed mass increased with increasing biomass, although in the high-density patches there was a leveling off at very high biomass levels (low-density patch: Pearson's $r = 0.83$, $P < 0.0001$; high-density patch: Pearson's $r = 0.73$, $P < 0.0001$). In low-density patches, $< 6\%$ of reproductive individuals produced more than one reproductive tiller; all reported density values were based on tiller number. In high-density cheatgrass patches reproductive tillers were not distinguished from the reproductive individual because tillering occurred rarely at high cheatgrass densities (Hulbert 1955; J. Beckstead, personal observation).

Three covariates with potential effects on cheatgrass biomass and density were measured at the time of harvest. First, for each plot in a low-density cheatgrass patch, we measured the distance to the nearest clump of five or more cheatgrass plants outside each plot. This measurement reflects the likelihood of seed additions to the plots from seed immigration (i.e., clumps closer to the plot indicate a greater probability of outside seed-input than clumps further away). This measure (hereafter, called additional seed-input) was used as a covariate to account for variation among plots in the natural addition of seeds in low-density patchs. This covariate does not account for seed additions derived from a seed bank. Second, herbivory, categorized as 'yes' (stem chewed to a stump) or 'no' (stem complete with reproductive structures), was assessed for one cheatgrass individual at each of 12 stratified points in each plot in both low- and high-density patches. The percentage of grazed individuals was used as a covariate to account for variation in herbivory on the response variables in both low- and high-density patches. This measure is an underestimate; it does not quantify herbivory to young plants prior to bolting or completely eaten plants. Third, native plant cover was estimated for each plot using modified Daubenmire cover classes (Mueller-Dombois and Ellenberg 1974). The midpoint of each cover class assigned to a plot was used as a covariate to separate the effects of the two components of the neighbor reduction treatment in low-density cheatgrass patches (i.e., to examine the clipping component independent of the selection of plots with lower native plant cover relative to controls; see model 2 below).

Statistical analyses

For each patch type separately, we analyzed differences in cheatgrass biomass and density as a mixed model analysis of covariance (ANCOVA), including stage, treatments nested within stage, control(s) at the patch level, and covariates as fixed effects and replication and replication by stage interaction as random effects (PROC MIXED; SAS 1999). PROC MIXED is recommended for mixed models and is based on restricted maximum likelihood estimation (REML) of linear statistical models involving both fixed and random effects (Steel et al. 1997).

The experiment was a two-factor nested design (stages and treatments nested within stage) with controls at the patch level. In model 1 for low-density cheatgrass patches, the two covariates were additional seed-input and herbivory. In model 2 for low-density patches, we repeated the analysis on a subset of data (neighbor reduction and control treatments) with two covariates, native plant cover and herbivory. Model 2 examined the clipping component independent of native plant cover in the neighbor reduction treatment. The covariate, additional seed-input, was not included as a covariate in model 2 because it was not significantly correlated with biomass and density in this subset of the data. For the high-density cheatgrass patches, level of herbivory was the only covariate.

Assumptions of ANCOVA were met following model selection procedures recommended by Littell et al. (1996). Appropriate transformations were performed when needed on variables to meet the assumption of normality. To compare

the resource treatments with the control(s), we used the one-tailed Dunnett test to correct for multiple comparisons with the same control (Zar 1999) on the least square means (to account for the appropriate standard errors).

Results

Herbivory/pathogen pressures

Nearly all plots sustained herbivory by grasshoppers (low-density patches, 94%; high-density patches, 100%). Mean herbivory per plot was significantly lower in low-density cheatgrass patches than in high-density patches (patch effect, ANOVA, $F = 6.55$, df = 1, 9, $P = 0.03$; low-density patches: $46 \pm 0.24\%$, mean $\pm$ 1 SD, $n = 220$; high-density patches: $59 \pm 0.15\%$, mean $\pm$ 1 SD, $n = 127$). Supporting this pattern, within both low- and high-density cheatgrass patches utilized in the field experiment, herbivory was higher in plots with greater biomass (low-density patches: Pearson's $r = 0.23$, $n = 240$, $P = 0.0003$; high-density patches: Pearson's $r = 0.51$, $n = 127$, $P = 0.0001$) and greater density (low-density patches: Pearson's $r = 0.47$, $n = 240$, $P = 0.0001$; high-density patches: Pearson's $r = 0.45$, $n = 127$, $P = 0.0001$).

Percentage smut infection per plot was slightly, but significantly, greater ($t = 2.33$, df = 52, $P = 0.02$) in low-density cheatgrass patches ($23 \pm 0.12\%$, mean $\pm$ 1 SD, $n = 30$) than in high-density patches ($17 \pm 0.08\%$, mean $\pm$ 1 SD, $n = 27$).

Increasing resources in low-density cheatgrass patches

Treatments nested within stage significantly increased cheatgrass biomass and density in low-density cheatgrass patches (Table 1; model 1). Overall, life stages did not differ significantly. Two of the three covariates, additional seed-input and herbivory, significantly influenced both biomass and density (Table 1). The significant relationship of additional seed-input indicates that plots closer to a seed source received additional seed-input, thus increasing cheatgrass measurements.

In model 1 for low-density cheatgrass patches, some treatments applied across all stages significantly increased cheatgrass biomass and/or density in comparison to the controls (Figure 2). Specifically, plots that received the combination treatment significantly increased biomass by 270% and density by 85%. Of the five individual treatments, reduced compaction had the strongest positive effect, significantly increasing biomass by 250% and density by 104%. Reduction of neighbors (native species) had the second strongest positive effect on both biomass and density, while adding nitrogen significantly increased biomass, but not density. Water and litter additions had no effects.

Some treatments applied at each life stage separately significantly increased cheatgrass biomass and/or density in comparison to the controls in Model 1 for low-density patches (Figure 2). Specifically, the combination treatment significantly increased biomass and density at only the active-growth stage. Neighbor reduction

Table 1. Model 1 for low-density cheatgrass patches: a nested ANCOVA for the effects of increasing resource availability on cheatgrass biomass and density.

Source	df	Biomass		Density	
		F	P	F	P
Stage	4, 36	1.92	0.13	1.58	0.20
Treatments nested within stage	17, 171	4.29	0.0001	3.34	0.0001
CoVar seed-input	1, 171	12.45	0.0005	15.67	0.0001
CoVar herbivory	1, 171	20.38	0.0001	83.94	0.0001

Treatments were applied at three life stages separately and across all stages.

The mixed-model was fit using SAS procedure MIXED and restricted maximum likelihood estimation. Covariance parameter estimates for the biomass model include rep = 0.003, rep × stage = 0.04, and residual = 0.19; the overall fit of the model contained a residual log-likelihood of −171.5. Covariance parameter estimates for the density model include rep = 0.005, rep × stage = 0.19, and residual = 0.48; the overall fit of the model contained a residual log-likelihood of −280.8.
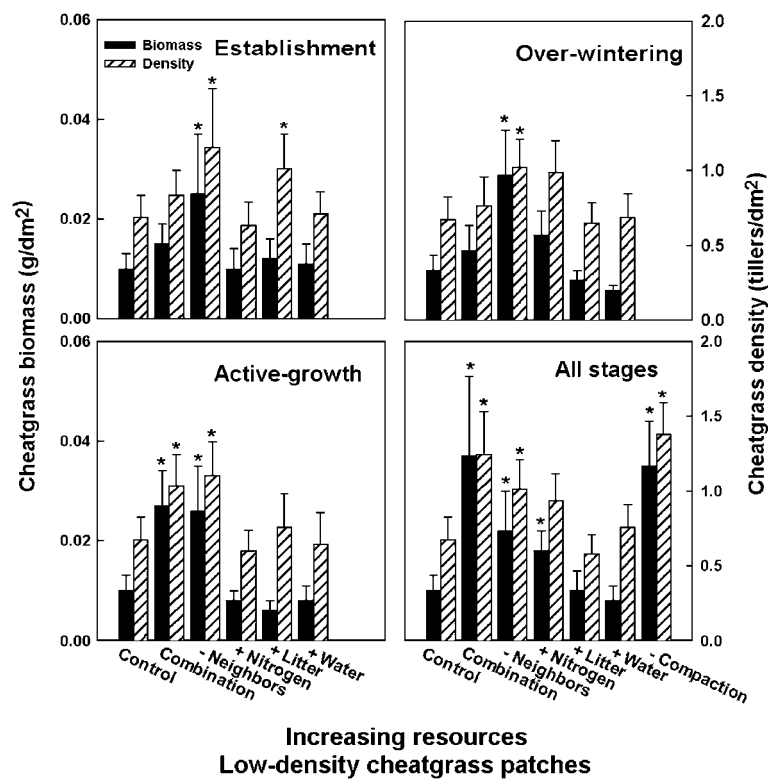
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Figure 2. Effect of resource treatments applied in low-density cheatgrass patches at three life stages separately and across all stages on cheatgrass biomass (left axis) and density (right axis) (means ± 1 SE). Resources were increased by adding (+) or reducing (−) factors. The combination treatment consisted of all treatments except soil compaction (see methods). Asterisks indicate a significant different (*P* < 0.05) between treatments and the control (1-tailed Dunnett test). Stages refer to time of application of treatment and not time of harvest. All plots were harvested at seed formation.

significantly increased both biomass and density at all three life stages. Litter addition significantly increased density, but not biomass, at only the establishment stage. Nitrogen and water additions had no significant effect at any life stage. When native plant cover was added as a covariate in model 2 (isolating the clipping effect of neighbors from the selection of plots with low native plant cover), the neighbor reduction treatment did not differ from the control for any life stage or across all stages (Table 2). Therefore, the significant effects of the neighbor reduction treatment in model 1 were due to the selection of plots with low native plant cover and not clipping *per se*, indicating that the effects of native plant cover persisted across all life stages.

Biomass increased more than density for nearly all treatments (e.g., reduced compaction

increased biomass by 250% and density by 104%; Figure 2). The only exception was that litter addition at establishment had no effect on biomass but increased density by 43%.

Decreasing resources in high-density cheatgrass patches

Treatments nested within stage significantly decreased cheatgrass biomass and density in high-density cheatgrass patches (Table 3). Overall, life stages did not differ significantly. The covariate, herbivory, significantly influenced both biomass and density (Table 3).

In high-density cheatgrass patches, some treatments applied across all stages significantly decreased cheatgrass biomass and/or density in comparison to the controls (Figure 3). Specifically, plots that received the combination

Table 2. Model 2 for low-density cheatgrass patches: an ANCOVA for the effects of increasing resource availability in the neighbor reduction and control treatments.

Source	df	Biomass		Density	
		F	*P*	*F*	*P*
Treatment (clipping)	4, 18	0.36	0.83	0.40	0.80
CoVar native plant cover	1, 18	4.71	0.044	4.46	0.049
CoVar herbivory	1, 18	15.88	0.0009	42.90	0.0001

This Model includes native plant cover as a covariate to separate the effects of the two components of the neighbor reduction treatment (i.e., to examine the clipping component independent of the selection of plots with lower native cover relative to controls) on cheatgrass biomass and density. The treatment was applied at three life stages separately and across all stages.
The mixed-model was fit using SAS procedure MIXED and restricted maximum likelihood estimation. Covariance parameter estimates for the biomass model include rep = 0.005, rep × stage = 0.17, and residual = 0.15; the overall fit of the model contained a residual log-likelihood of −60.9. Covariance parameter estimates for the density model include rep = 0.0, rep × stage = 0.09, and residual = 0.55; the overall fit of the model contained a residual log-likelihood of −86.4.

treatment significantly decreased density by 35% compared to the controls, but not biomass. Of the three individual treatments, reduced nitrogen had the strongest negative effect, significantly decreasing density by 37%, but not biomass. Litter reduction and compaction enhancement had no effects.

Some treatments applied at each life stage separately significantly decreased cheatgrass biomass and/or density in comparison to the controls in high-density patches (Figure 3). Specifically, the combination treatment significantly decreased biomass and density at the over-wintering and active-growth stage (treatment not applied at establishment stage). Nitrogen reduction significantly reduced both biomass and density at the establishment and active-growth stage, but not at the over-wintering stage. Litter reduction significantly decreased biomass and density at the establishment stage. At the over-wintering stage litter reduction significantly decreased only density; while at the active-growth stage, it had no effect.

Discussion

Herbivore/pathogen pressures

Invasion biology hypotheses suggest that enemies (predators/parasites) acquired in the invaded range increase invasion resistance (biotic resistance hypothesis; for review see Maron and Vilà 2001). This study demonstrates that even if an introduced species is utilized as a food source in the invaded range, such as cheatgrass eaten by North American grasshoppers (primarily *Xanthippus corallipes* and *Melanoplus confusus*), the herbivores may be ineffective at restricting the population growth of the invasive species. Herbivory quantified in this study does not explain resistance patterns of low- and high-density cheatgrass patches; contrary to resistance patterns, low-density cheatgrass patches sustained significantly less herbivory than the high-density patches. Supporting this, in both low and high-density patches, herbivory on cheatgrass was higher with greater cheatgrass biomass and

Table 3. Nested ANCOVA for the effects of decreasing resource availability in high-density cheatgrass patches on cheatgrass biomass and density.

Source	df	Biomass		Density	
		F	*P*	*F*	*P*
Stage	4, 36	2.18	0.09	2.15	0.10
Treatments nested within stage	8, 68	2.61	0.01	2.27	0.03
CoVar herbivory	1, 68	14.43	0.0003	10.38	0.002

Treatments were applied at three life stages separately and across all stages.
The mixed-model was fit using SAS procedure MIXED and restricted maximum likelihood estimation. Covariance parameter estimates for the biomass model include rep = 0.03, rep × stage = 0.04, and residual = 0.06; the overall fit of the model contained a residual log-likelihood of −46.7. Covariance parameter estimates for the density model include rep = 3.11, rep × stage = 3.62, and residual = 9.29; the overall fit of the model contained a residual log-likelihood of −321.6.
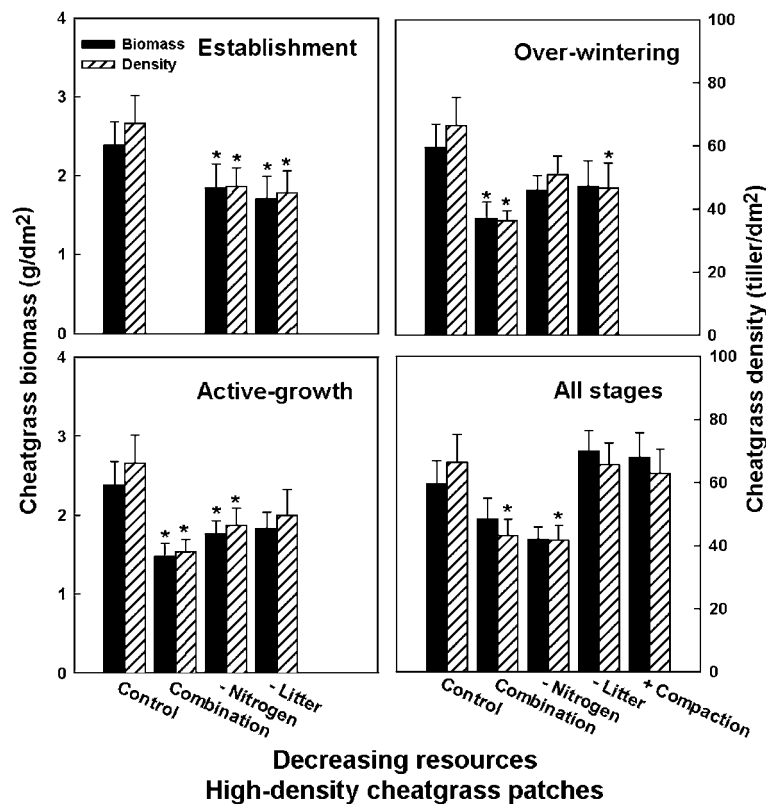
Figure 3. Effect of resource treatments applied in high-density cheatgrass patches at three life stages separately and across all stages combined on cheatgrass biomass (left axis) and density (right axis) (means ± 1 SE). Resources were decreased by adding (+) or reducing (−) factors. The combination treatment consisted of all treatments except soil compaction (see 'Materials and methods'). The combination treatment was not applied at the establishment stage. Asterisks indicate a significant different ($P < 0.05$) between treatments and the control (1-tailed Dunnett test). Stages refer to time of application of treatment and not time of harvest. All plots were harvested at seed formation

density. As previously noted, the abundance of Mormon crickets was reduced by selective insecticidal bait and therefore the effects of this migrating herbivore are unknown. If the Mormon crickets had not been chemically controlled, it is possible that herbivory levels would have been much higher and overshadowed any treatment effects. Although the short-term effects of these herbivores on cheatgrass can be substantial, their long-term and large-scale effects on the population dynamics of cheatgrass are unexplored. Although high smut infection can occur in cheatgrass (>90%; Klemmedson and Smith 1964), this study does not indicate that pathogen pressure explains the resistance patterns of low- vs high-density cheatgrass patches. Percent smut infection was significantly different, but not very high in either low- (23%) or high- (17%) density cheat-

grass patches. It is unlikely that these low levels of smut infection could influence seed production to such an extent to account for the large differences of cheatgrass biomass and density found in the low- and high-density cheatgrass patches.

Increasing resources in low-density cheatgrass patches

Reduction in soil compaction in low-density cheatgrass patches resulted in the greatest increase in cheatgrass biomass and density, indicating that resources are present, but physically unavailable to cheatgrass. We do not know the precise mechanism(s) by which compaction made resources unavailable to cheatgrass in this study. A reduction in soil compaction is associated most likely with an increase in macropores, which

favor high infiltration rates (Blackburn 1975) and soil aeration (Arshad et al. 1996). Indirectly, reduced soil compaction can result in a flush of nutrients, as a result of increased mineralization rates due to higher water and oxygen availability to microbes (Hassink et al. 1993). Hobbs (1989) predicted that disturbance enhances invasibility only if it increases the availability of a limiting resource. Increasing resource availability to invasive species through a physical soil disturbance is often linked with the removal of competitors (e.g., by animal disturbance; Platt 1975; Hobbs and Mooney 1985) or a relatively intense disturbance combined with nutrient inputs (Hobbs and Atkins 1988; Burke and Grime 1996). This study is unique in that it offers an example of a change in resistance to invasion due solely to a relatively mild disturbance (reduced compaction treatment resulted in aeration of top 5 cm; see 'Materials and methods') that is not linked to the removal of competitors.

The doubling of cheatgrass density by the reduced compaction treatment may be explained by an increase in survival due to an increase in the variety or number of safe sites (Harper 1977). Seeds in the reduced compaction plots may have become partially buried during rainfall in depressions created by the manipulation and thus experienced a different microenvironment than seeds in the undisturbed control plots. Although safe sites may explain the increase in density, the tripling effect on cheatgrass biomass can be explained only by an increase in resource availability. Therefore, due either to nutrient availability and/or safe site availability, these results predict that any disturbance that reduces soil compaction in low-density cheatgrass patches will result in reduced site resistance and a subsequent increase in cheatgrass invasion.

Removal of competitors by a disturbance is often considered the primary factor leading to invasion success (Crawley 1987; Hobbs 1989). We found that a reduction of neighbors (native grasses) in low-density cheatgrass patches significantly increased cheatgrass biomass and density, indicating the importance of competition in limiting cheatgrass at this spatial scale. Removal of native competitors by grazing is considered the fundamental way in which cheatgrass initially became invasive in the western US (Mack 1981),

although repeated fires are acknowledged today as the primary mode for large-scale spread (Knapp 1996). Although clipping of neighbors did not increase cheatgrass biomass or density, selected plots with lower native plant cover than the controls had increased cheatgrass biomass and density. This finding indicates that areas with low native plant cover contain resources not exploited by competitors and, therefore, they experience greater susceptibility to cheatgrass invasion.

Nitrogen and water are considered the most limiting resources in semi-arid desert systems (West 1991). We found nitrogen addition in low-density cheatgrass patches increased cheatgrass biomass and density when applied across all stages; however, we found no effect from the water addition treatment. Similarly, Link et al. (1995) and Cline and Rickard (1973) found nitrogen to be more limiting than soil moisture to cheatgrass biomass in the field. If this one-year experiment had been conducted under drought conditions, the results may have been different.

Reducing resources in high-density cheatgrass patches

Reduction of nitrogen *via* sucrose addition in high-density cheatgrass patches significantly reduced cheatgrass biomass and density, indicating the importance of nitrogen availability in maintaining cheatgrass production in these less resistant patches. Similarly, McLendon and Redente (1991) found in a semi-arid sagebrush community that a reduction of nitrogen *via* sucrose addition resulted in less competitive and productive cheatgrass plants, resulting in a compositional shift to perennial grasses and forbs. Their results were most pronounced when soil moisture was high (McLendon and Redente 1992). In addition, we found that a combination of nitrogen reduction and litter removal (likely reducing water availability) led to the largest reduction of cheatgrass biomass and density during the overwintering and active-growth stages of cheatgrass.

Comparing reciprocal resource treatments in both patch types

We found that low- and high-density cheatgrass patches represent variation in resistance

maintained by differential resource availability. However, the specific resources and the extent to which they regulate cheatgrass may not be the same in both low- and high-density cheatgrass patches. Although reducing nitrogen had a strong effect in maintaining site susceptibility in high-density cheatgrass patches, nitrogen addition had a weaker effect on overcoming site resistance in low-density cheatgrass patches. Likewise, degree of compaction had a large effect in low-density patches, but no significant effect in high-density patches. These conflicting results may be an artifact of the strength of the manipulation. Alternatively, they may indicate that nitrogen is of greater importance in maintaining high-density cheatgrass patches and soil compaction is of greater importance in maintaining low-density patches. Further factorial experiments that vary resource strength would be necessary to clarify this point.

For both low- and high-density cheatgrass patches, we found that life stages of cheatgrass were differentially affected by the resource manipulations. In low-density patches, litter addition increased density at only the establishment stage. Similarly, Pierson and Mack (1990) found that a thin layer of litter increased germination and seedling survival. This increase in density, but not biomass, indicates that survival is enhanced with litter addition, likely due to the water retention ability of litter (Stewart and Hull 1949) and a decrease in secondary seed dispersal (Pierson and Mack 1990). In high-density patches, litter reduction reduced cheatgrass at both the establishment and over-wintering stages. Again, the water retention ability of litter and the effects of litter on secondary dispersal explain these effects at the establishment stage. At the over-wintering stage, litter may have acted as insulation, buffering plants from extreme temperatures. Also, in high-density patches, nitrogen reduction reduced cheatgrass at the establishment and active-growth stage, but not at the over-wintering stage. Bilbrough and Caldwell (1997) found that cheatgrass tiller production increased with nitrogen pulses during the early vegetative growth stage, when growth rates were high, such as the active-growth stage. The unique response of each life stage to the resource manipulations may indicate different resource requirements of each stage (Schupp 1995) or the ability of the plant to exploit the resources at that time interval (Bilbrough and Caldwell 1997).

Conclusions

The strong density and biomass responses obtained by manipulating resources in both low- and high-density cheatgrass patches indicate that resource availability is critical in maintaining this local-scale variation. Thus the difference in density can be interpreted as a reflection of variation in resistance due to variation in resources. Continued resistance to cheatgrass invasion within low-density cheatgrass patches is dependent on maintaining conditions that will not drastically increase the availability of resources. Resources are not the only factors that could influence the local-scale variation in cheatgrass density. We found no indication, however, that seed limitation, independent of resources, was sufficient to account for the low-density cheatgrass patches (Beckstead 2001) nor did we find that patterns of herbivory/pathogen pressures corresponded with the variation in resistance patterns. It is possible that factors not tested, such as history of local-scale disturbance (see origin discussion below) could play a complementary role in connection with resource availability in maintaining the local-scale variation in resistance.

Although this study does not determine what force(s) originally created the high-density cheatgrass patches, these results suggest that it may have been a local disturbance that reduced soil compaction and/or native species. Similar to this prediction and at a similar local scale, Hobbs and Mooney (1991) found that the patchy mosaic of annual grasses in a serpentine grassland reflected past soil disturbance by pocket gophers. Common local soil disturbances at this study site are pocket gopher mounds and digging from coyotes/foxes at the base of shrubs (J. Beckstead, personal observation). Both of these soil disturbances reduce native species and soil compaction. In addition, digging at the shrub base kills the shrubs. Shrub death most likely increases local soil fertility, in accordance with shrubs acting as 'islands of fertility' (Crawford and Gosz 1982; Noy-Meir 1985). These findings, in connection with this study, predict that any local disturbance in low-density cheatgrass patches that kills shrubs, in addition to

reducing native grasses and soil compaction, will increase resource availability resulting in increased cheatgrass biomass and density. Overall, this study provides strong evidence that variation in natural resistance within this shadscale-bunch-grass community in western Utah is maintained *via* differential resource availability.

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